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An Alternative Interpretation

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16. ABSTRACT

Grossman argued that communities can be classified as either deterministic or stochastic. Deterministic communities are characterized by persistence(or succession toward a climax) while communities that lack these properties are stochastic. These descriptors were intended to replace the terms equilibrium and nonequilibrium, respectively.

Grossman et al.(1982) used this conceptual framework to examine fish collections taken over a 12 yr. period from one stream site in Indiana. They defined community persistence as significant correlation in ranked abundances of 10 seasonally most abundant species, measured with Kendall's coefficient of concordance. Because this test showed no significant similarity among autumn samples, they concluded that this community was not persistent and that "this assemblage is probably regulated by stochastic factors".

We disagree with this conclusion. In choices of study site, sample method, replication, emphasized season, and analytical approach, we believe Grossman et al. took options most likely to show variability. Other reasonable options would have indicated less variability, or even led to the opposite conclusion. Furthermore, variablility in relative abundances is not sufficient evidence for control of communities by stochastic processes.

17. KEY WORDS AND DOCUMENT ANALYSIS

a. DESCRIPTORS	b. IDENTIFIERS/OPEN ENDED TERMS	c. COSATI Field/Group

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NOTES AND COMMENTS

STOCHASTICITY IN STREAM FISH COMMUNITIES: AN ALTERNATIVE INTERPRETATION

Grossman (1982*a*) argued that communities can be classified as either deterministic or stochastic. Deterministic communities (*sensu* Grossman) are characterized by persistence (or succession toward a climax) while communities that lack these properties are stochastic. These descriptors were intended to replace the terms equilibrium and nonequilibrium, respectively.

Grossman et al. (1982) used this conceptual framework to examine fish collections taken over a 12-yr period from one stream site in Indiana (Whitaker 1976). They defined community persistence as significant correlation in ranked abundances of 10 seasonally most abundant species, measured with Kendall's coefficient of concordance. Because this test showed no significant similarity among autumn samples (see Grossman 1982*b*), they concluded that this community was not persistent and that "this assemblage is probably regulated by stochastic factors" (Grossman et al. 1982, p. 438).

We disagree with this conclusion. In choices of study site, sample method, replication, emphasized season, and analytical approach, we believe Grossman et al. took options most likely to show variability. Other reasonable options would have indicated less variability, or even led to the opposite conclusion, i.e., the community was temporally persistent. Furthermore, variability in relative abundances is not sufficient evidence for control of communities by stochastic processes.

Study site.—A 120-m section of Otter Creek located below a dam and within 5 km of its confluence with the Wabash River was sampled over an extended period, apparently because it generally yielded more species of fishes than other sites in that area (Whitaker 1976; Whitaker and Wallace 1973). Reasons suggested for this high fish diversity (Whitaker 1976) include high habitat diversity (substrate type, depth, and current) and proximity to the Wabash River. As an illustration of the latter effect, Whitaker and Wallace (1973) found an average of 20.9 species per collection at the dam, compared to 9.9 per collection in the stream above the dam. Species not found above the dam were called river species. In addition, the dam may concentrate species, since only 15.7 species were caught per collection at downstream sites within Otter Creek. Therefore, this site is not typical of others in that watershed.

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Methods.—Little was reported of sampling methods by either Whitaker (1976) or Grossman et al. (1982). Nothing was said regarding adequacy of sampling other than that effort varied with water level. We do not know if variation in numbers of fish collected was due to differences in sampling effort and efficiency, differences in abundance, or both. However, seining was in an upstream direction, contrary to standard practice (Hendricks et al. 1980). Seining upstream yields fewer individuals and fewer species with different ranked abundances than the more usual downstream seining (Paloumpis 1958). An important determinant of sampling efficiency for different fish size classes is seine mesh size, but we do not know the mesh size used or whether it varied among samples. However, net mesh was apparently small enough to allow collection of young-of-the-year fish, at least in autumn (Grossman et al. 1982, table 1). This probably accounts for the observed peak abundances of common species in autumn (Whitaker 1976).

Inclusion of young-of-the-year with older fish introduces two problems. First, abundance of this age class is most strongly affected by environmental conditions (Pflieger 1975; Serns 1982; Schlosser 1982*b*; Waters 1982), and variation in this numerically dominant age class could swamp constancy in older classes. Second, all fish, regardless of sizes, are counted and summed alike. In the case of *Notropis chrysocephalus*, for example, this meant including individuals with a potential range in length of 10 to 180 mm (Smith 1979) and range in mass much larger. The young-of-the-year, following a type III mortality curve, are only temporarily abundant. Because of early summer spawning by most of these fish and higher expected variability of young-of-the-year abundances than that of older age classes, we expect year-to-year variability to increase from spring to fall (Schlosser 1982*a*), the pattern observed by Grossman et al. (1982, table 2).

Fish mobility and community scale.—The authors based their expectation of community constancy on the observation that at their study site "habitat appeared to retain a stable physiognomic character; no major changes were noted in its structure" (Grossman et al. 1982, p. 425). Then, in order to establish that within this constant habitat "sampling encompassed an actual assemblage or . . . a random segment from an assemblage" (p. 426) they proposed that "individuals of the majority of species collected would have spent a great proportion of their lives within the study site" (p. 426). Of the references cited in support, only Gerking (1959) explicitly dealt with restricted movements of fish. However, in reviewing the relevant literature up to 1959, Gerking did not find any cyprinid showing such restricted movements, and the majority of common species in Otter Creek were cyprinids.

Whitaker (1976) implied that individuals of at least two common species (*Notropis atherinoides* and *N. spilopterus*) moved to the site from the Wabash River, and other studies indicate cyprinids in streams are unlikely to remain within a 120-m site (Ruhr 1956; Moshenko and Gee 1973; Fraser and Sise 1980; Storck and Momot 1981). Indeed, Grossman et al. later remark on migration (table 1) and vagility (p. 431) of stream fishes.

The likely movement of fish into and out of the study site is important for two reasons. The first is that Grossman et al. assume a deterministic community should remain constant only if the habitat is constant. They state that the habitat

was constant at the study site, but they have no knowledge of the habitat in other parts of the stream where the fish may have spent significant portions of their lives. Second, movement of fish introduces questions about the scale which should be considered in investigating community constancy or variability. Grossman et al. assume that fish stay within 120 m and that this is an appropriate unit of study. If fish move routinely throughout the 5 km of stream between the dam and the Wabash River, this 5-km section may be the appropriate unit. Although we cannot suggest the most appropriate scale for examination of community constancy in this stream, available information suggests that the scale chosen by Grossman et al. may be too small.

Analysis of data.—Grossman et al. assumed between-sample differences reflected actual between-year differences in the fish community. Although they collected more than one sample per season in some years, they did not compare the variability between these samples with the variability found between samples taken in different years. Each sample was not a complete census, but included sampling error (p. 427) and possible variability caused by short-term differences in the fish present at the site. Examination of the magnitude of these sources of variability is necessary to evaluate between-year variation. Seven pairs of samples were collected in the same year and season. We calculated concordances in ranked abundances (Conover 1980) of the same 10 common species used by Grossman et al. and found that one of the three pairs of summer samples and two of the four pairs of autumn samples were not significantly similar. Therefore, although samples taken in different years had different ranks of common species, so did some replicate samples taken in the same month or the same season. At least some of the year-to-year variability could have resulted from short-term or sampling variability.

The authors made two contestable choices in their analysis of community persistence. First, they defined community persistence as concordance in ranked abundances of species, citing Harrison (1979) who, however, defined persistence as maintenance of population levels "within acceptable ranges," not as constancy of relative abundances. Another criterion for persistence might be similarity in species occurrence through time. Second, they restricted their analysis to 10 species caught in greatest total number in each season. They could have chosen a different number of species to consider, such as the 18 species identified as "major" by Whitaker (1976). We show the effects of these different approaches.

To examine the occurrence of species through time, we compared the number of species shared between two collections with the number expected had the second collection been an independent draw from a species pool, following the method of Gotelli and Abele (1982; see our Appendix A). The species pool may be variously defined as those species collected in the season, all species collected at the site, or all species from the region. We analyzed the first two situations, which are more likely than the last to indicate randomness. In all cases, the actual number of shared species was no fewer than the number expected at random, and usually many more. For example (table 1), there were 120 paired comparisons for autumn collections. These pairs shared an average of 16 species out of an average 23 per collection, seven more than would have been shared if each collection were

TABLE 1

SHARED SPECIES AND RANKED ABUNDANCES PER SEASON

	Spring	Summer	Autumn
Pairs of samples	6	21	120
Species pool (N)	26	40	55
Range of S_o	6–13	13–22	10–21
Range of S_E	4.2–12.3	9.9–20.6	5.8–13.0
Mean ($S_o - S_E$)	1.1	2.9	6.6
Mean n	14	24	23
Sample years	4	5	12
For 10 most common species			
Concordance	.408	.390	.121
P	.10	.05	.20
For 18 major species			
Concordance	.678	.522	.194
P	.001	.001	.01

NOTE.—Observed species shared between samples (S_o) compared to expected (S_E) based on species pool N (n = species per collection).

a random draw from the 55 species collected in autumn. From two to 10 more shared species than expected were present. Furthermore, the number of shared species did not decrease with increasing time between samples, as one would expect if species composition followed a random walk. Therefore, if the question of community persistence were posed as "Does one tend to find the same species from year to year?" the answer would be "Yes."

Although it is reasonable to exclude rare species from the analysis, the choice of which species to include is necessarily arbitrary. When the 18 "major" species (Whitaker 1976) are considered for each season, concordance increased from that found for only 10 species (table 1). As before, the concordances were highest in spring, intermediate in summer, and lowest in autumn. Therefore, the analytical approach of Grossman et al. is sensitive to the number of species included. Analysis of the larger species pool leads to the conclusion that community structure, as measured by rank order abundances, is persistent from year to year.

Summarizing these two results, the test for species similarity showed that certain species were more likely to be found at this site from year to year than were other local species and the concordance test showed that certain species tended to be more abundant at the site than were other species. Grossman et al.'s analysis showed, on the other hand, that none of the 10 most common autumn species was reliably more abundant than the others.

Grossman et al. also considered persistence of trophic structure by categorizing species into one or more trophic groups and examining year-to-year differences in numerical percentages of the groups. Other investigators have defined such categories differently (e.g., Horwitz 1978; Schlosser 1982*b*) but the present state of knowledge allows uncertainty as to proper categorization. In addition, fish of different sizes, both within and among species, were again combined. We are most concerned, however, that the data were analyzed as percentages of the collection rather than as numbers. Analysis of percents was apparently done to

TABLE 2

ANOVA OF SUMMER TROPHIC GROUPS

Source	df	MS
Trophic groups	7	13.838***
Sample dates	6	1.413
Error	42	1.020

*** $P < .001$.

control for sample size, on the assumption that in larger samples each trophic group increased proportionately. If this assumption does not hold, for example, if the trophic groups vary independently, use of percentages introduces statistical dependence on sample size (Hills 1978) and also results in the appearance of variation in all groups whenever only one varies.

We analyzed the trophic structure of summer collections with two-way ANOVA of log-transformed counts with the eight categories defined by Grossman et al. Differences in sizes of trophic groups across the seven collections taken in 5 yr were highly significant (table 2). Therefore, relative sizes of the trophic groups tended to be similar among samples through this period. That is, trophic structure of the community showed year-to-year persistence.

Collection and analysis of data always involve choices (Green 1979). Choices made in collection of data especially affect conclusions that can be drawn. In each case of choice of location, choice of sample method, choice of replication, choice of season to emphasize, and choice of analytical approach, Grossman et al. reasonably could have taken other options that might have indicated less variability. More importantly, other reasonable choices of data analysis lead to the qualitatively opposite conclusion that the community was temporally persistent.

Nonetheless, year-to-year variation in fish abundance is well known (Watt 1968; Pella 1979; Serns 1982; Skud 1982; Toth et al. 1982; Waters 1982; references cited by Grossman et al. 1982). Thus, changes in abundances discussed by Grossman et al. are expected. We disagree, however, with the interpretation put on such change by these authors in the context of general ecological theory.

Stochastic versus deterministic assemblages.—We strongly disagree with the use of the terms stochastic and deterministic by Grossman et al. (1982) and Grossman (1982*a*). They equate equilibrium with deterministic (with the exception that succession may be deterministic) and develop from this definition the prediction that nonsuccessional deterministic communities have invariant community structure. They also equate nonequilibrium with stochastic, and use the converse of their prediction for deterministic communities to identify stochastic communities. That is, all nonsuccessional communities with variable community structure are stochastic communities. Use of these two terms, and the predictions from them, are contrary to accepted usage in biology, and, we believe, hinder biological understanding.

A stochastic process is one whose outcome is ultimately unpredictable, within some universe of possible results. The common nonbiological example is the die. Knowledge of conditions at the time a die is thrown will never allow accurate

prediction of the outcome. A deterministic process is one whose outcome is ultimately predictable, given knowledge of initial or prevailing conditions. This outcome need not be equilibrium, even if conditions do not change, for example, cycles, oscillations, and chaos (May 1974; May and Oster 1976). Temporal variability is especially characteristic of age-structured populations not at equilibrium (Charlesworth 1980). Parameters of deterministic processes may reflect known relationships between environmental factors and biological characteristics such as growth, mortality, or competitive ability (Park 1954; Watt 1968; Serns 1982; Skud 1982; Baltz et al. 1982). Known, or knowable, changes in environmental factors can result in predictable variations in the outcomes.

A stochastic process is different from a deterministic process that includes as parameters variables with stochastic characteristics. Through time, the outcome of the strictly stochastic process continues to be unpredictable, regardless of knowledge of prevailing conditions, while the outcome of the deterministic process can be predictable with that knowledge. Alternatively, identification of a process as deterministic, but dependent on known but variable environmental conditions, can lead to useful predictions of outcomes at locations where the range of environmental conditions differ. Temporal variability in communities is often interpretable given knowledge of the physical environment, for such varied groups as fish (Toth et al. 1982), birds (Kendeigh 1982; Karr and Freemark 1983), and insects (Kendeigh 1979). Spatial differences in fish communities have also been examined from this perspective (e.g., Baltz et al. 1982).

As an illustration, consider the three equations below:

$$Y = \epsilon \tag{1}$$

$$Y = \bar{Y} + \epsilon \tag{2}$$

$$Y = f(X) + \epsilon \tag{3}$$

where ϵ is a random variate of unknown distribution. These expressions could represent any ecological characteristic, such as population size of a species, and the X-variate could be an environmental characteristic such as temperature. The random variate, ϵ, may include sampling variability in addition to actual variability, but for now assume it includes only the latter. Strictly, each equation presents Y as stochastically controlled because of the inclusion of ϵ. However, if the size of the standard deviation of ϵ is not large compared to $\bar{Y}$ or $f(X)$ then Y can be largely predictable. If X is also a random variate, then its distribution and boundedness will determine the distribution and boundedness of Y. Equating (2) and (3) with (1) because each contains ϵ is an oversimplification resulting in considerable loss of information.

We see three major disadvantages to failure to distinguish deterministic processes with stochastic environmental parameters from purely stochastic processes. First, factors that are presently unpredictable may be predictable in the future. Second, factors that are unpredictable over a short time period may have a long-term trend (e.g., mean annual temperature, Pella 1979). Third, organisms may not find these factors as unpredictable as we do, may move in response to shifting conditions (Karr and Freemark 1983), or may respond physiologically or genetically. As an example of the last, Matthews and Styron (1981) found fish in

more variable habitats to be physiologically less sensitive to environmental variation.

In addition, labeling a process stochastic when it is in fact deterministic, but with stochastic parameters, discourages investigation of mechanisms leading to apparent stochasticity. For example, although Grossman et al. (1982) discuss the possible effects of environmental variability (p. 436), they chose not to examine their data in light of available weather records, but apparently were satisfied to label the community stochastic.

In addition to denying that temporal variability implies stochasticity, we also deny that a response ". . . to environmental conditions in a species-specific, rather than an assemblage-specific manner . . . implies that interactive processes such as resource partitioning may be unimportant . . ." (Grossman et al. 1982, p. 437). They present the view that deterministic processes imply that the community must behave as a unit. This perception of the community has been abandoned on empirical grounds (see, e.g., Whittaker 1975) and, more recently, on theoretical grounds (May 1975). Theory (May 1981) suggests that strong connectance should occur only among small numbers of species. Therefore, species within different groups should respond independently of each other, and responses of species within a group should be more closely related but still a function of the species' individual attributes.

Hypothesis testing.—Grossman et al. apparently set out to prove a null hypothesis and did so to their satisfaction (p. 429). Their comment notwithstanding, it is epistemologically impossible to accept a null hypothesis; one can only reject it or fail to reject it (Strong 1980). At best, one can entertain a null hypothesis after repeated rejection of all likely alternatives (Strong 1980), but the preferred procedure is to accept a hypothesis only after failure of attempts to falsify it. Grossman et al. accepted their hypothesis after they had falsified a single different hypothesis. Statistically, the null hypothesis is assumed until data force its rejection in favor of the hypothesis being tested. The probability of incorrectly rejecting the alternative hypothesis (type II error) is not tightly controlled and may be larger than the probability of incorrectly rejecting the null hypothesis (type I error, Sokal and Rohlf 1969). Since one begins by assuming the null hypothesis and also tolerates higher rates of type II error, failure to reject the null hypothesis is weak evidence of its truth.

A biological hypothesis is not tested directly; instead a prediction from a hypothesis is tested. Therefore, in order to choose among competing hypotheses, each must lead to sufficiently distinct predictions. In this case, the prediction from their null hypothesis (stochastic control of community structure) was that relative numbers of common species change from year to year. Since this can also be a prediction of the alternative hypothesis (deterministic control), it cannot be used to distinguish the two hypotheses. Other possible predictions of their null hypothesis might be temporal variability in relative abundances of all species, dissimilarity in species composition with increasing time, and high temporal variability in the number of species. The data were not consistent with any of these predictions.

Conclusion.—In summary, aspects of site selection and collecting techniques indicate the site studied by Grossman et al. may not be typical of streams in that

area and the data may have been biased toward showing community variability. Further analysis of the data they presented shows a higher than expected constancy in species composition at this site with much similarity in species and trophic group abundances among years. These are not attributes of a "stochastic" community.

We do agree with Grossman et al. that climatic effects on stream fish population sizes are important. We also agree that these communities may never be at an equilibrium and that this can have important implications for community dynamics and for evolution. We disagree, however, with the perception of the extent of temporal variation. We are impressed with how little, rather than with how much, variation there is given profound environmental variation. We also disagree that variation in a nonsuccessional community must indicate that biological interactions are unimportant. Most of all, we disagree with their terminology, which combines unrelated processes and phenomena, discourages investigation of mechanisms, and conceals important functional aspects of the system.

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APPENDIX A

The expected number of species shared between two collections was based on random sampling without replacement, using the equation:

$$S_E = \frac{n_1 n_2}{N} \tag{1}$$

where S_E is the expected number of shared species; n_i is the observed number of species in the ith collection; and N is the size of the species pool. The probability of two collections' sharing y or fewer species can be found by:

$$P(X \leq y) = \frac{\sum_{x=0}^{y} \binom{n_1}{x}\binom{N - n_1}{n_2 - x}}{\binom{N}{n_2}} \tag{2}$$

and the probability of two collections' sharing y or more species can be found by:

$$P(X \geq y) = 1 - P(X \leq y - 1). \tag{3}$$

These calculations assume that the two collections are independent draws from the species pool and that all species are equally likely to be drawn. Greater numbers of shared species than expected suggest either lack of independence between collections or differences among species in the likelihood of being included in collections.

The size of S_E is dependent on n_1, n_2 and N. Only the choice of N is arbitrary. If N is small (e.g., $N = n_1 + n_2$), S_E will be large; if N is large (e.g., all species in the region), S_E will be small. The two n_i's are taken as observed, and if either is large, S_E will be large and even large observed S_o will be indistinguishable from random in (3).

Finally, the randomness of shared species S_o is tested in (3), not the observed n_1 and n_2. For example, in the nonrandom case where $n_i = N$ for all i, S_o ($= n_i$) would always be the randomly expected S_E. Therefore, while deviations from randomness may be real (with appropriate N), apparent lack of deviation from randomness should be interpreted cautiously.

In the analysis of shared species, S_E was calculated for all pairs of collections made within a season. Because of the form of (1), S_E is the same whichever collection is designated n_1.

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